# Rapid visuomotor feedback gains are tuned to the task dynamics

Abbreviated title: Adaptation involves visuomotor feedback modulation

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**Abstract (246/250 words)**

Adaptation to novel dynamics requires learning a motor memory, or a new pattern of predictive feedforward motor commands. Recently we demonstrated the up-regulation of rapid visuomotor feedback gains early in curl force field learning, which decrease once a predictive motor memory is learned. However, even after learning is complete, these feedback gains are higher than those observed in the null field trials. Interestingly these up-regulated feedback gains in the curl field were not observed in a constant force field. We therefore suggest that adaptation also involves selectively tuning the feedback sensitivity of the sensorimotor control system to the environment. Here we test this hypothesis by measuring the rapid visuomotor feedback gains after subjects adapt to a variety of novel dynamics generated by a robotic manipulandum in three experiments. To probe the feedback gains, we measured the magnitude of the motor response to rapid shifts in the visual location of the hand during reaching. While the feedback gain magnitude remained similar over a larger than a four-fold increase in constant background load, the feedback gains scaled with increasing lateral resistance and increasing instability. The third experiment demonstrated that the feedback gains could also be independently tuned to perturbations to the left and right depending on the lateral resistance, demonstrating the fractionation of feedback gains to environmental dynamics. Our results demonstrate that the sensorimotor control system regulates the gain of the feedback system as part of the adaptation process to novel dynamics, appropriately tuning them to the environment.

**New & Noteworthy**

Here we test whether rapid visuomotor feedback responses are selectively tuned to the task dynamics. The responses do not exhibit gain scaling, but do vary with the level and stability of task dynamics. Moreover these feedback gains are independently tuned to perturbations

to the left and right, depending on these dynamics. Our results demonstrate that the sensorimotor control system regulates the feedback gain as part of the adaptation process, tuning them appropriately to the environment.

## Introduction

We constantly interact with our environment, be it playing sports or drinking a cup of coffee. In order to produce skilled movements, unaffected by these dynamic interactions, we need to predict the task dynamics and adapt our control strategy accordingly. It has been shown that the sensorimotor control system builds a predictive feedforward controller of the internal and external dynamics (Lackner and DiZio 1994; Shadmehr and Mussa-Ivaldi 1994; Conditt et al. 1997; Goodbody and Wolpert 1998; Kluzik et al. 2008). This feedforward controller predictively generates the appropriate pattern of muscle activation that compensates for the dynamics of the environment and generalizes these predictions across a variety of kinematics and limb states. A sudden change in task dynamics during the movement causes kinematic errors, leading to large increases in muscle co-contraction (Thoroughman and Shadmehr 1999; Franklin et al. 2003) and feedback gains (Franklin et al. 2012; Cluff and Scott 2013). These reactive responses act to limit the perturbing effects of the new dynamics until the sensorimotor control system is able to learn a new internal model, or adapt the previous model, that can predictively compensate for this change in dynamics. Once the internal model is updated, the reactive responses are gradually decreased (Franklin et al. 2012) along with the co-contraction (Franklin et al. 2003).

Feedback corrections to errors during reaching can arise through both muscle stretch dependent motor responses (stretch reflexes) (Bennett 1994; Kurtzer et al. 2009; Nashed et al. 2014) and rapid visuomotor responses responding to shifts in the visual location of the hand (Sarlegna et al. 2003; Saunders and Knill 2003; Franklin and Wolpert 2008), the target

(Goodale et al. 1986; Brenner and Smeets 1997; Day and Lyon 2000; Oostwoud Wijdenes et al. 2011; Hayashi et al. 2016) or the visual background (Saijo et al. 2005; Abekawa and Gomi 2015). These visuomotor responses are involuntary in nature (Day and Lyon 2000; Franklin and Wolpert 2008; Gomi 2008) with loop delays to force production on the order of 150 ms (Franklin et al. 2016). Insights into the control of such involuntary responses may provide important insight into voluntary control (Franklin and Wolpert 2011) as it has been suggested that the same neural circuitry underlying such rapid motor responses is also involved in voluntary control (Pruszynski et al. 2011a) as proposed by the optimal feedback control framework (Todorov and Jordan 2002; Scott 2004; Todorov 2004).

In our previous work, we proposed that the large changes in rapid visuomotor feedback gains during initial learning resulted from the increased uncertainty in the internal model (Franklin et al. 2012). We demonstrated increased rapid visuomotor feedback gains early in curl force field learning, which decreased once the predictive motor memory was learned. However, even after learning, these feedback gains remained high compared to those in null field trials. Moreover these up-regulated feedback gains in the curl field were not observed in with constant background loads. We propose that these final levels of feedback gains were not simply increased according to the uncertainty, but were actually adapted and tuned to the task dynamics. We propose that the changes in feedback gain seen in this previous work highlight two computational components of feedback modulation: reactive control and predictive control. The reactive control produces an initial (likely generalized) increase in feedback gains in response to uncertainty in the environment (Franklin et al. 2012), and parallels the rise in co-contraction (Osu et al. 2002; Franklin et al. 2003, 2012; Darainy and Ostry 2008). In contrast, the predictive controller gradually tunes and adapts the feedback gains appropriately for the environmental dynamics as learning proceeds (Cluff and Scott 2013). Therefore adaptation does not only involve learning a set of predictive muscle activation patterns but also learning to selectively tune the feedback sensitivity of the sensorimotor control system to the environment. This is supported by studies showing that

stretch-dependent feedback responses are modified for movements in stable (Wagner and Smith 2008; Ahmadi-Pajouh et al. 2012; Cluff and Scott 2013) and unstable dynamics (Franklin et al. 2007), although some results are confounded by gain scaling (Pruszynski et al. 2009). Similarly visuomotor feedback responses have been show to modify with changes in the visuomotor mapping (Franklin and Wolpert 2008; Franklin et al. 2014; Hayashi et al. 2016). However, these studies have examined feedback modulation under a limited set of experimental conditions, such as a single force field, making it difficult to determine the degree to which the feedback gains can be modulated. Here we expand upon these results, examining how the visuomotor feedback gains adapt to different characteristics of the environmental dynamics. Specifically we examine how the predictive visuomotor feedback gains scale across a broader range of background loads, different types of force fields, and in particular for force fields with asymmetric dynamics. That is, we examine whether or not these learned feedback responses can match the asymmetry of the environmental dynamics.

## Materials and Methods

Seventeen subjects provided written informed consent, and participated in the experiments which were approved by the Cambridge Psychology Research Ethics Committee. All subjects were right-handed according to the Edinburgh handedness inventory (Oldfield 1971) with no reported neurological disorders. Subjects were allocated to the three experiments (n=8, 10 & 8) where each subjects participated in either one or two of the experiments.

*Apparatus.*

Subjects were seated with their shoulders restrained against the back of a chair by a shoulder harness and grasped the handle of the vBOT robotic manipulandum (Howard et al.

2009) with their forearm supported against gravity with an air sled (Fig 1A). The robotic manipulandum both generated the environmental dynamics (null field, force field or channel), and measured the subjects' behavior. Position and force data were sampled at 1KHz. Endpoint forces at the handle were measured using an ATI Nano 25 6-axis force-torque transducer (ATI Industrial Automation, NC, USA). The position of the vBOT handle was calculated from joint-position sensors (58SA; IED) on the motor axes. Visual feedback was provided using a computer monitor mounted above the vBOT and projected veridically to the subject via a mirror. This virtual reality system covers the manipulandum, arm and hand of the subject, preventing any visual information about their location. The exact time that the stimuli were presented visually to the subjects was determined using the video card refresh rate and confirmed with an optical sensor to measure any time delays. Subjects performed right-handed forward reaching movements in the horizontal plane at approximately 10 cm below their shoulder level.

*Experimental Setup.*

Movements were made from a 1 cm diameter start circle centered approximately 28 cm in front of the subject to a 2 cm diameter target circle centered 25 cm in front of the start circle. The subject's arm was hidden from view by the virtual reality visual system, which displayed the start and target circles as well as a 0.6 cm diameter cursor representing the hand position. A successful movement required the hand cursor to enter the target (without overshooting) within 700 ± 75 ms of movement initiation. Overshoot was defined as movements that exceeded the target in the direction of movement. When subjects performed a successful movement they were provided with feedback of how close they were to the desired movement time of 700 ms ('great' if within ± 37.5 ms, otherwise 'good') and the counter increased. When they performed unsuccessful movements they were provided with feedback as to why the movement was not considered successful ("too fast", "too slow" or "overshot target") and the counter remained at the previous value. All trials were recorded regardless of their success. The initiation of trials was self paced; subjects initiated a trial by

moving the hand cursor into the start circle and holding it within the target for 1000 ms. A tone then indicated that the subjects could begin the movement to the target. The duration of the movement was determined from the time that the hand cursor exited the start circle until the time that the cursor entered the final target.

*Probe trials to measure feedback gains.*

In order to assess rapid visuomotor feedback magnitude, visually induced motor responses were examined using perturbations of the visual system similar to those previously described (Franklin and Wolpert 2008; Dimitriou et al. 2013; Reichenbach et al. 2014; Franklin et al. 2016). On random probe trials, when the hand had moved a specific percentage of the distance to the target (e.g. 20% or 5 cm) the cursor representing the hand position was jumped away from the current hand position, held 2 cm away laterally from the actual hand trajectory for 250 ms and then returned to the actual hand position for the rest of the movement (Fig 1B). The direction of the jump (left vs right) was randomized across trials. During these trials, the hand was physically constrained to the straight path between the initial starting position and the final target using a mechanical channel, such that any force produced in response to the visual perturbation can be measured against the channel wall using the force sensor. The mechanical wall of the channel was implemented with a stiffness of 5,000 N/m and damping of 10 $N \bullet m^{-1} \bullet s$ for any movement lateral to the straight line joining the starting location and the middle of the target (Scheidt et al. 2000; Milner and Franklin 2005). As this visual perturbation is transitory with the cursor returning to match the actual hand position, subjects are not required to respond to this visual perturbation to produce a successful trial. These visual perturbations were applied perpendicular to the direction of the movement (either to the left or the right). For comparison a zero perturbation trial was also included in which the hand was held to a straight-line trajectory to the target but the visual cursor remained at the hand position throughout the trial. The perturbation trials were

randomly applied during movements in a blocked fashion such that one of each of the three perturbations were applied within a block of trials. A non-probe trial movement was always performed first in any new phase such that a probe trial was never the first movement.

*Experimental Paradigm.*

Three experiments were performed to examine whether the rapid visuomotor feedback gains are adapted to the dynamics of the external environment after adaptation.

*Experiment 1: visuomotor gains under a resistive background load*

Eight subjects participated in this experiment (2 female: aged 29.1 ± 6.7, mean ± SD) in which we extend our previous finding (Franklin et al. 2012) that the rapid visuomotor feedback gain does not increase with an externally applied constant background load. Previously we applied forces orthogonal to the line between the start and target locations. In this experiment the background load was applied in the direction opposite to the movement, that is along the line joining start and target location. The three visual perturbation or probe trials (rightward +2.0 cm, zero or leftward -2.0 cm) were presented pseudo-randomly within a single block of 9 trials (3 probe trials and 6 visually unperturbed trials) in order to assess the visuomotor response. The onset of the displacements occurred at 5 cm from the start of the movement (20% of the length of the movement). Each probe trial was repeated 30 times for each background force level.

In the experiment, on every trial a constant force was applied in the direction opposite (*-y*) to the direction of movement. The constant force was experienced at six levels (3, 5, 7, 9, 11 and 13N) where all the trials at a particular force level were blocked together. The order of the blocks of constant forces was randomized across subjects. Subjects performed the experiment in two sessions in which three of the force levels were experienced in each session. For each force level, 271 trials (of which 90 were probe trials) were performed.

Subjects were required to take short breaks every 100 movements throughout the experiment. They were also allowed to rest at any point they wished. To initiate a trial, subjects moved into the start circle and then the background load ramped up over 300 ms. Once the desired background load was achieved and subjects had stabilized their hand within the start circle for 1000 ms, a tone indicated that the subject should perform the reaching movement to the target. Once subjects had maintained the hand within the target circle for 400 ms, the background force was ramped back down over 300 ms. Throughout the movement the background force level and direction were constant in Cartesian space.

*Experiment 2: visuomotor gains under a viscous force fields*

Ten subjects participated in the second experiment (3 female: aged 28.5 ± 6.1) examining the role of viscous force fields on the rapid visuomotor feedback gains. Our previous work (Franklin et al. 2012) demonstrated that the introduction of a viscous force field had two effects: an initial increase in feedback gains related to the magnitude of the kinematic error and an increased final level of feedback gain relative to the level in the null field. This second increase in the feedback gain after extensive learning was proposed to arise through an adaptation of the feedback gain to the increased uncertainty in the environment due to the interaction between signal-dependent noise and a velocity dependent force field (Franklin et al. 2012). This possibility arises as muscle activation increases during adaptation causing an appropriate increase in motor noise. Both motor noise and planning noise (Churchland et al. 2006; van Beers 2009) would cause an increase in the trial-by-trial variability. The actual forces produced by the force field depend entirely on the specific trajectory performed, thus variability in the trajectory increases the variability in the applied forces, increasing the uncertainty of the environment and state of the limb. In order to examine whether the final plateau level of feedback gains is truly adapted to the environmental dynamics we examined the final adaptation to five different environmental dynamics. Subjects adapted to each force field in a randomized order across subjects in a single session on one day. The background

force field was modulated in two ways relative to a baseline resistive force field: the magnitude of the field and degree of stability. The baseline force field was a resistive viscous field:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} -b & 0 \\ 0 & -b \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix}$$

where *b* was 30 N•m$^{-1}$•s (Fig 1 C; middle).

In order to examine the degree to which the rapid visuomotor feedback response scaled with the magnitude of the force field, the constant *b* was changed for two environments: either decreased to 15 N•m$^{-1}$•s or increased to 45 N•m$^{-1}$•s (Fig 1C top and bottom). All three force fields are stable, however each force field would be expected to influence the visuomotor reflex differently if the sensorimotor control system adapts the visuomotor reflex to the task dynamics. Specifically, the resistance in the direction orthogonal to the movement increases, therefore if the hand had been actually perturbed by the size of the visual perturbation, then a smaller or larger amount of restoring force respectively is required to bring the hand back to the original movement for the lower and higher resistive force fields.

In order to examine the effect of stability in the external environments, two further force fields were examined where the stability was only manipulated in the direction orthogonal to the forward reaching movement. The stable force field had the addition of a mechanical channel in the lateral direction with stiffness of 50 N•m$^{-1}$ and viscosity of 10 N•m$^{-1}$•s, with no change in the forward reaching direction (Fig 1C left). Specifically this was implemented as:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} -b & 0 \\ 0 & -10 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} + \begin{bmatrix} -50 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix}$$

where the value of *b* was the same as for the baseline field (30 N•m$^{-1}$•s). The unstable field had an assistive viscous element in the direction orthogonal to the direction of motion (Fig 1C right) and was implemented as:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} -b & 0 \\ 0 & 10 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix}.$$

where the value of *b* was the same as for the baseline field (30 N•m$^{-1}$•s).

As in the first experiment subjects performed 271 trials in each condition, comprised of 90 probe trials (30 rightward, 30 zero and 30 leftward probes) and 181 trials in the specific force field. In all probe trials, while the lateral forces were constrained by the channel, the forces in the direction of the movement were those of the condition (e.g. resistive viscous field). While lateral movement in the random probe trials was constrained by the mechanical channel, the subjects were free to move in any manner during all of the other trials. All other conditions were the same as in the first experiment, except that subjects did not need to wait for a background force to be ramped up or down at the beginning or end of each trial.

*Experiment 3: rapid visuomotor feedback gains for asymmetric fields*

Eight subjects participated in the third experiment (6 female: aged 23.5 ± 3.8) investigating whether the visuomotor feedback gain could be independently modulated for leftward and rightward perturbations if the force field produced different forces to leftwards and rightwards motion. Our previous work (Franklin et al. 2014) has shown that the late visuomotor feedback gains can be independently modulated to leftwards and rightwards perturbations when different task-relevant or task-irrelevant sensory discrepancies are applied to the left or right of the movement. Here we further investigate this issue in order to determine whether these visuomotor feedback gains also modulate independently to leftward or rightward

perturbations according to the dynamics of the environment. Three different environmental conditions were studied which varied in terms of the lateral viscous component all of which were implemented as:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} b_1 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \text{ if } \dot{x} \geq 0$$

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = \begin{bmatrix} b_2 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \text{ if } \dot{x} < 0$$

The equal condition was implemented as $b_1 = b_2 = -20$ (N•m$^{-1}$•s) such that the field provided equal resistance to movements with positive or negative *x*-velocity and no resistance in the *y*-axis (Fig 2A). The strong leftwards resistance condition (Fig 2B) was implemented as $b_1 = 0$ and $b_2 = -40$ (N•m$^{-1}$•s) whereas the strong rightwards resistance condition (Fig 2C) was implemented as $b_1 = -40$ and $b_2 = 0$ (N•m$^{-1}$•s). Subjects were split randomly into two equal sized groups, where both groups started with the equal resistance condition. One group then performed the strong rightwards resistance condition followed by the strong leftwards condition whereas the other group performed these two in the opposite order.

Each condition consisted of 50 blocks where each block consisted of 10 trials (500 trials total). As in the previous two experiments, each block consisted of 3 probe trials (rightward +2 cm, zero or leftward -2 cm) presented pseudo-randomly in which lateral motion was constrained by a mechanical channel (Fig 2E). The other trials in the block consisted of trials in which the visual cursor was shifted laterally by one of seven magnitudes [-6.0, -4.0, -2.0, 0.0, 2.0, 4.0, 6.0] cm and held at this distance for the remainder of the trial (Fig 2D). This ensured that subjects experienced the forces which are not apparent if they made a perfectly straight movement to the target. Subjects were therefore required to compensate for the imposed visual displacement in order to bring the cursor into the target by the end of the

movement (Franklin et al. 2016). All probe trials and maintained visual perturbations occurred at 12.5 cm from the start position (50% of the movement distance). The onset of the visual perturbations was set to the middle of the movement as the rapid visuomotor feedback gain is highest at this point during the movement (Dimitriou et al. 2013), as predicted by optimal feedback control theory (Liu and Todorov 2007). The cursor was 1.0 cm in diameter, start circle was 1.4 cm in diameter and target circle was 1.6 cm in diameter. Short rest breaks were required every 200 trials, although movements were self-paced throughout the experiment allowing subjects to take breaks at any point. All other details were matched to experiment 2.

**Analysis**

Analysis of the experimental data was performed using MATLAB R2015a. Position, velocity and endpoint force were low-pass filtered at 40Hz with a fifth-order, zero phase-lag Butterworth filter. Acceleration was calculated by differentiating the filtered velocity. Repeated measures ANOVAs were performed in MATLAB using the ranova function. If a significant main effect of force field was found, planned multiple comparisons between the responses in each of the force fields (multcompare function) were performed using the Tukey-Kramer method. When appropriate, linear regression was performed for each subject using the mean responses for each condition. The slopes across subjects were then examined using a t-test to determine if the slopes were significantly different from zero. Statistical significance was considered at the $p<0.05$ level for all statistical tests.

The purpose of the study was to examine the relation between the task dynamics and the feedback gains after adaptation. In order to examine adaptation to the task we calculated several kinematic and descriptive parameters over the training period. For each measure we calculated the mean across all force fields or loads as a function of the block number. The

results were used to determine the period over which these measures became stable so that we could use this period to examine the feedback gains after learning. Based on this analysis we omitted the first five blocks as these measures changed rapidly during this phase. After removing the first 5 blocks of trials, the mean response (and standard error of the mean) for each condition was calculated and plotted.

*Hand path error.* The maximum perpendicular error (MPE) of the hand was used as a measure of the straightness of the hand trajectory. The MPE is the maximum distance on the actual trajectory that the hand reaches perpendicular to the straight-line path joining the start and end circles (errors to the left are defined as negative and errors to the right are defined as positive). The MPE was calculated for each non-probe trial throughout the learning experiment.

*Success Rate.* Each movement was designated a successful trial if the subject performed the movement within the desired time (700 ± 75 ms) and did not overshoot the target.

*Movement Duration.* The movement duration was calculated as the time between the subject leaving the start circle and first entering the target circle as long as they maintained their position within the final target circle for 400 ms. If the subject passed through the target, overshooting the target completely, then the duration included this overshoot up to the point at which subjects entered the target and were able to stabilize within the target.

*Peak Velocity.* The peak velocity was calculated as the maximum velocity in the direction of movement (y-axis) that occurred between the subject leaving the start circle and first entering the target circle.

*Rapid visuomotor responses.* Individual probe trials were aligned on visual perturbation onset. The response to the right visual perturbation (or left visual perturbation) on probe

trials was subtracted from the response on zero probe trials in order to provide two estimates of the motor response to the visual perturbation for each block. Depending on the experiment these were either averaged (experiments 1 and 2) or analyzed separately (experiment 3). Visuomotor responses from the first 5 blocks of each experiment were not used in the analysis. To examine the feedback gain, we calculated the average post-perturbation force over two intervals: the first corresponding to a rapid involuntary response (180–230 ms) (Franklin and Wolpert 2008), and the second to a slower response (230-300 ms) which may be a mixture of involuntary and voluntary responses. The early interval was conservatively determined (Franklin and Wolpert 2008) using a voluntary reaction task (Day and Lyon 2000) to determine an interval which avoided any voluntary responses.

For the third experiment, ROC analysis (Pruszynski et al. 2008) was performed in order to determine the earliest time at which visuomotor responses were modulated independently for perturbations in the force fields. Specifically, in order to examine whether there was independent modulation of the feedback responses for different force fields and determine the time that such independent modulation occurs, we generated an ROC curve for every 1 ms sample. That is we calculated the area under the ROC (aROC) curves for the ability to distinguish between the responses to the same perturbation in the rightwards resistive field and the leftwards resistive field. The discrimination time was taken as the point when the aROC exceed 0.75 for three consecutive samples. As we are interested in the time point where this difference emerges in the force responses, we examine the time point where the information begins to deviate from chance (Thompson et al. 1996). To do this we excluded aROC after the discrimination point and fit a dog leg to the aROC data (flat line at aROC of 0.5 followed by a linear component). The time of the end of the flat portion of the fit was taken as the onset time of the response (Pruszynski et al. 2008). The ROC analysis was performed using the individual data for each subject separately as well as across the subjects using the mean traces for each subject.

405

406 **Results**

407

408 We examined the modulation of visuomotor responses to environmental dynamics in three
409 separate experiments. In each experiment the background dynamics were modulated in
410 order to test whether the rapid visuomotor feedback gains modulate across these changes in
411 the environment. In each dynamical environment, subjects performed reaching movements
412 while grasping the handle of a robotic manipulandum (Fig 1A). The rapid visuomotor
413 feedback gains were then measured on randomly selected trials (termed probe trials) during
414 which the visual cursor, representing the hand position, was perturbed while the physical
415 hand was mechanically constrained to move within a channel to the target. These
416 visuomotor perturbations were orthogonal to the channel either to the left or right (Fig 1B,
417 2E), and resulted in an involuntary motor response producing force against the channel wall.
418 This change in lateral force was quantified over appropriate temporal windows to estimate
419 the feedback gain.

420

421 *Experiment 1. visuomotor gains under a background load*

422

423 The first experiment was designed to further examine changes in rapid visuomotor feedback
424 gains that might occur with a constant background load. In a previous study we showed that
425 constant *lateral* forces produce no increase in the rapid visuomotor feedback gain over a
426 small range of force levels (Franklin et al. 2012). Here we used probe trials to measure the
427 rapid visuomotor feedback responses with different levels of constant background force [3,
428 5, 7, 9, 11 and 13 N] where the forces were applied *along* the direction of motion, that is
429 opposite to motion and, therefore, orthogonal to the forces in our previous study. This
430 direction of background load corresponds to the direction of increased loading due to the
431 resistive fields used in experiment 2. Subjects rapidly learned to produce consistent
432 movements with the background load with minimal kinematic errors and a high success rate

(Fig 3). Figure 3 shows that subjects performed stably after the first 5 blocks when a new background force was introduced (Fig 3, black lines). We therefore used the last 25 blocks to examine the visuomotor gain, which showed little variance between conditions (Fig 3, colored error bars).

The response to the perturbation shows clear force responses for all six force levels (Fig 4A) with a peak in the force around 250 ms after the onset of the perturbation (Fig 4B). Although there were no dramatic differences in the force traces, the highest background force levels appeared to have the slightly larger force responses. This was investigated by determining the mean visuomotor force response over both the initial involuntary feedback window (180-230 ms) and a later interval (230-300ms) (Fig 4B,C). The results of a repeated measures ANOVA with main factor of condition (6 levels) showed no significant main effect of force level for either the early ($F_{5,35}$=1.44; p=0.233) or late ($F_{5,35}$=0.971; p=0.448) intervals.

Similar to previous studies (Saijo et al. 2005), we also performed linear regression on the mean data for each subject separately to examine gain scaling. We compared the slopes across subjects with a t-test in order to determine if the slopes were significantly different from zero. The slopes for the early interval (0.0241 ± 0.031; mean ± std) were not significantly different than zero ($t_7$=2.21; p=0.063). This was also true to the late interval where the slopes (0.0211 ± 0.036; mean ± std) were not significantly different than zero ($t_7$=1.62; p=0.15). Therefore, despite more than a four-fold increase in background force level, there were no significant differences in the rapid visuomotor feedback gain across the conditions. This remained true even when the perturbations to the left and the perturbations to the right were separately examined (Fig 3E-G) within a single repeated measures ANOVA with main factors of condition (6 levels) and perturbation direction (2 levels). We found no significant main effect of condition ($F_{5,35}$=1.444; p=0.233), perturbation direction ($F_{1,7}$=0.560; p=0.479) or interaction effect ($F_{5,35}$=1.430; p=0.238) for the early interval. Similarly we found no significant main effect of condition ($F_{5,35}$=0.971; p=0.449), perturbation direction

($F_{1,7}$=0.163; p=0.699) or interaction effect ($F_{5,35}$=1.071; p=0.393) for the late interval. Overall there were no significant differences in the magnitude of the response to leftward and rightward perturbations regardless of loading conditions.

These results, combined with our previous finding (Franklin et al. 2012), suggests that the rapid visuomotor feedback responses do not exhibit the gain scaling to background force, unlike the short latency stretch reflex responses (Pruszynski et al. 2009). In particular, the resistive force fields in the next experiment (experiment 2) require larger forces in the direction of motion. Here we show that higher forces in this direction produce limited effects on the visuomotor feedback responses, and therefore that any differences are unlikely to be explained by this factor.

*Experiment 2. visuomotor gains under a viscous force fields*

Our previous study found that even after learning a velocity-dependent force field, the rapid visuomotor feedback gain was increased relative to that seen in a null force field (Franklin et al. 2012) which suggested that the rapid visuomotor feedback gains might be adapted to the environmental dynamics. The second experiment tested this possibility by investigating whether the rapid visuomotor feedback responses scaled with changes in the magnitude and type of force field. Subjects adapted to three different levels of a resistive viscous force field (Fig 1C middle column; -15, -30 and -45 $N \bullet m^{-1} \bullet s$) as well as two force fields where the stability was manipulated in the direction orthogonal to the reach direction (Fig 5C left and right fields). Stable performance in terms of kinematic error and duration were found by the fifth block of trials (Fig 5), so we again analyzed the last 25 blocks. As expected, there were differences between the conditions on these measures (Fig 5, colored error bars), with the unstable condition having the lowest success rate and largest MPE. However the peak velocity was similar across all conditions.

As the resistive viscosity increased, the feedback response on the probe trials also increased (Fig. 6A, light to dark blue). The magnitude of these responses was examined over the two intervals using an ANOVA with main effect of force field and random effect of subjects. There was a significant increase in the feedback response for both the early ($F_{2,18}$=6.799; p=0.006) and late ($F_{2,18}$=9.273; p=0.002) intervals. After significant main effects, the post-hoc comparisons indicated that the feedback responses were significantly different for the -15 N•m$^{-1}$•s field compared to both the -30 (p=0.046) and -45 N•m$^{-1}$•s (p=0.009) fields, but there was no significant difference between the two highest force fields (p=0.64) during the early interval (Fig. 6B). This effect was maintained in the late interval, with significant differences between the -15 N•m$^{-1}$•s field and the -30 (p=0.011) and -45 N•m$^{-1}$•s (p=0.011) fields, and no difference (p=0.394) between the two highest fields (Fig. 6C). However, similar to experiment 1, we performed linear regression for each subject. In contrast to the previous experiment, here we found that the slopes between the force response and the force field value were significantly different from zero for both the early ($t_9$=3.88; p=0.0037) and late intervals ($t_9$=3.77; p=0.0044). Thus as the resistive force field increased in strength, the visuomotor response gain also increased.

Three conditions (Fig 1D, middle row) in the experiment were matched in terms of the forces in the forward direction with a resistive viscous force of -30 N•m$^{-1}$•s (the middle field above). One field (Fig 1D middle) was uniformly resistive in all directions, while the other two varied in the stability in the direction orthogonal to movement. The more stable fields was constrained to always be in a mechanical channel, while the less stable field was assistive in

511 the orthogonal direction and hence unstable (+10 $N \bullet m^{-1} \bullet s$). Despite the same forward
512 resistance to motion, the feedback responses showed strong differences in their amplitudes
513 (Fig 6D). Again there were significant main effects of force field on the feedback gains for
514 both the early ($F_{2,18}$=8.869; p=0.002) and late ($F_{2,18}$=9.841; p=0.0013) time intervals. Post
515 hoc comparisons indicated that the feedback response in the mechanical channel was
516 significantly smaller than the unstable force field (p=0.003), but no differences between the
517 resistive fields responses and the unstable (p=0.11) or channel fields (p=0.12) for the early
518 interval (Fig 6E). At the later window, the channel was significantly different from both the
519 resistive (p=0.028) and unstable (p=0.015) force fields (Fig 6F).
520
521 *Experiment 3. rapid visuomotor feedback gains for asymmetric fields*
522
523 The previous experiment showed that the rapid visuomotor feedback responses vary
524 appropriately depending on the force field in which subjects made their movements. As the
525 first experiment demonstrated that constant forces, and therefore simple changes in
526 background load, do not affect the feedback gains, the results of the second experiment
527 suggested that the rapid visuomotor feedback gains adapt to the force field in order to
528 provide an appropriate compensation for the dynamics. In the third experiment we test this
529 possibility directly by introducing force fields that only have a lateral component orthogonal
530 to the direction of movement. Specifically we examine the feedback gains in three force
531 fields in which the appropriate feedback response to a perturbation to the left or right of
532 straight reaching movement would vary. The fields were either equal on both sides of the
533 reach direction, strongly resistive to leftwards motion or strongly resistive to rightwards
534 motion (Fig 2A-C). Subjects made reaching movements in all three fields in a blocked
535 design. In each field, along with probe trials to measure feedback gains, on non-probe trials
536 the cursor was shifted laterally to one of seven locations (ranging from -6 to +6 cm) and the

subjects were required to compensate for the shift by the end of the movement so that the cursor entered the target (Fig 2D). These visual shifts were included to ensure participants experienced the lateral forces over the workspace. It is important to note that the majority of the trials are ones in which a cursor jump is present. The velocity-dependent resistive force fields therefore make it more difficult to return the cursor to the midline. While the maximum perpendicular error and peak velocity changed little throughout the adaptation, the success rate increased and the duration decreased (Fig 7). It can be seen from the figure that the major effect on performance was within the first five blocks, with a much more gradual improvement in performance after these initial movements. The first five blocks of trials were therefore not analyzed in terms of the visuomotor gain. Differences between the conditions were small (Fig 7, colored error bars).

The majority of trials (70%) were ones in which the cursor was shifted laterally by up to 6 cm and subjects had to compensate for the shift, bringing the cursor towards the target. However in each field, the required force in order to produce this action varied, particularly for movements rightward or leftward. Adaptation, therefore, required subjects to produce different amounts of corrective force in the three force fields. We start by examining the corrective responses of these trials to shifts in the cursor. After a cursor jump, subject made corrective movement under all fields, bringing the cursor back toward the target (Fig 8A, F & K). In the symmetric force field, the lateral acceleration in response to the shift in visual hand position increased proportional to the magnitude and direction of the shift (Fig 8B). The onset of the change in acceleration started approximately 150 ms after the visual shift, a response time equivalent to the normal visuomotor feedback delays (Franklin and Wolpert 2008; Reichenbach et al. 2009; Franklin et al. 2016). The mean acceleration was then examined over a 100 ms interval (180-280 ms). It can be seen that the kinematic responses to leftward and rightward shifts were approximately equal as expected (Fig 8C). These roughly equivalent responses in terms of kinematics were also seen for the leftwards resistive (Fig 8G & H) and rightwards resistive force fields (Fig 8L & M). However, if the

kinematics were similar but force fields are different, then the sensorimotor system must have changed the force response to a given size of visual shift. This was investigated by looking at the lateral hand force (measured with the force transducer at the handle) in each of the three fields (Fig 8D, I & N). It is apparent that the early force responses are adapted appropriately to the force fields with increased force responses to rightwards perturbations in the leftward resistive field (Fig 8J) with no accompanying increase in the response to leftward perturbations (larger magnitude dark reds compared to light reds). Note that a rightward cursor perturbation requires a leftward compensatory motion to get to the target, and therefore the subject would experience the high resistive force in this direction for this force field. The opposite response (large forces in response to leftward perturbations) is seen in the rightward resistive force field (Fig 8O, larger responses for light blue compared to dark blue). Finally, in the equal resistive field, the responses to perturbations in either direction were similar (Fig 8E). These results show that the corrective responses have been appropriately adapted to each of the three force fields over the initial 100 ms of response. In particular, it also demonstrates that these corrective responses can be independently controlled to the right or left of the straight reaching movement.

However, the previous results are based on measurements of the kinematics and force responses in freely moving trials making it difficult to examine the exact time course of the corrective responses. Therefore, throughout the experiments subjects were also presented with probe trials (brief visual shifts with a mechanical channel resisting changes in lateral motion) in order to measure the feedback gains. The force responses to these probe perturbations were examined relative to a zero perturbation condition for all three force fields (Fig 9A). Over the full time period, clear differences could be seen in the responses, with movements in the block with the leftward resistive field (red) showing larger responses to rightward perturbations than the equal (green) or rightward (blue) resistive fields. For leftward perturbations the responses were reversed with the leftward resistive field showing the small responses (orange), followed by the equal condition (light green) and largest

response in the rightward resistive field (light blue). The mean feedback force was then quantified over both the early and late intervals (Fig 9B). In the early interval, while it appeared there may be an effect of the force field, the main effect of force field in the ANOVA failed to reach significance for either perturbations to the right ($F_{2,14}$=2.966; p=0.084) or left ($F_{2,14}$=2.915; p=0.087) of the reaching movement. However, for the later interval (Fig 9B) there were significant main effects for perturbations to the right ($F_{2,14}$=11.159; p=0.0013) and to the left ($F_{2,14}$=8.431; p=0.004). Post-hoc tests found significant differences between the rightwards and leftwards fields for both the rightward perturbation (p=0.007) and the leftward perturbation (p=0.025). For both the right and left perturbations we found significant slopes ($t_7$=4.498; p=0.003 and $t_7$=3.461; p=0.011 respectively) at the late interval, but only for the right perturbation at the early interval ($t_7$=2.962; p=0.021).

These analyses showed that the modulation of the responses to the perturbations are changed by the late interval, however it did not allow us to examine at what time point they become significantly different. We used ROC analysis (Pruszynski et al. 2008) in order to look at the time point when the responses each perturbation direction in the rightwards and leftwards resistive fields could be distinguished relative to the baseline equal condition (see Methods). For the leftward perturbation (Fig 9C) this occurred at 169 ms (large red circle) and for rightward perturbations (Fig 9D) this occurred at 158 ms (large red circle). We also calculated the onset times for each subject individually (small circles). The estimated time point at which the significance difference begins were consistently earlier than the earliest measure of voluntary feedback (230 ms) that was seen for a single subject in a previous study (Franklin and Wolpert 2008) and far before the estimated voluntary response time (265 ms) for similar perturbations (Kobak and Mehring 2012). This suggests that complex patterns of feedback gains, which vary on one-side of a reaching movement compared to the other, can be controlled according to the dynamics of the environment within involuntary time windows.

## Discussion

The adaptation of rapid visuomotor feedback gains to temporal changes in the environmental dynamics was examined during reaching movements. We found that the magnitude of these feedback gains was not affected by increases in a constant background load (over a fourfold range) opposing the direction of movement. However, in a second experiment, the feedback gains scaled strongly with changes in the viscous environment, increasing as the resistive force field increased. Moreover, the feedback gains also varied as the lateral component alone changed, increasing in a laterally unstable field while decreasing when stability and lateral accuracy was guaranteed (mechanical channel). These results suggested that the rapid visuomotor feedback gains adapt to the environment as part of the learning process. In order to examine this, we conducted a third experiment in which we examined this effect more precisely by introducing force fields which vary in the required responses to perturbation to the right or left of a reaching movement. The results showed that the relative feedback responses to leftward and rightward perturbations are clearly changed in the late interval period, with initial differing responses occurring within the involuntary time window. These modulated feedback responses were appropriated modified to the dynamics of the external environment; larger when higher resistive forces would have been present. Overall, our results demonstrate that dynamic adaptation not only involves learning the predictive feedforward control of muscle activity but also involves the tuning of feedback gains to the novel environment.

While the short latency stretch reflex responses have long been known to exhibit scaling with background muscle activity or automatic gain scaling (Bedingham and Tatton 1984; Matthews 1986; Pruszynski et al. 2009), this was not found for rapid visuomotor feedback responses elicited by shifts in the visual hand position (Franklin et al. 2012). Here we further

examined this issue by using larger background loads (up to 13N constant load) in the direction of reaching. Again we found little change in the feedback magnitude over the wide range of constant loads examined, with responses of a similar magnitude to those of our previous study. This further suggests that these responses do not exhibit such gain scaling. In short latency stretch reflexes, the gain scaling is thought to result from the organization of the motoneuron pool where the motor units are recruited according to their force generating capability or size (Henneman 1957; Marsden et al. 1976; Capaday and Stein 1987). However, later responses gradually show reduced gain scaling (Pruszynski et al. 2009) until there is no effect for steady state voluntary control (Milner-Brown and Stein 1975), suggesting that the sensorimotor control system compensates for the non-linear recruitment of the motoneuron pool. This decrease in the gain scaling is well matched with the timing of increased cortical contributions to the long latency responses (Pruszynski et al. 2011a, 2011b) and the subsequent sophistication of these feedback responses (Kurtzer et al. 2008; Nashed et al. 2014). The absence of gain scaling in the visuomotor responses also suggests that a similar model of the motoneuron pool recruitment process must be used to adapt the commands to the underlying background muscle activity. However, it is not clear whether this arises through cortical processing of the motor commands as some evidence has suggested a subcortical pathway for the earliest visuomotor responses through the colliculus (Reynolds and Day 2012). It is important to note that in our experiments, we have only examined the force responses (feedback gains) as a function of the background load, rather than examine the muscular responses using electromyography. While this technique may miss subtle effects that could be seen in the muscle activity, it also provides a comprehensive overall response of all muscles that could be responding to the perturbation. In contrast, analysis of the electromyographic activity only samples a subset of the muscles and motor units that contribute to the overall response. Although we cannot claim a definitive test of the gain-scaling within this paper, it is clear that larger forces in the direction of motion have limited effects on the visuomotor feedback gain. In particular, a four-fold change in load produced at most a 20% (n.s.) increase in the rapid visuomotor response. Thus we can

claim that any changes seen in experiment 2 are unlikely to be affected by the small changes in loading that occur within these studies.

The absence of any evidence of gain scaling for visuomotor responses contrasts with the results for the manual following response or MFR (Saijo et al. 2005; Gomi et al. 2006; Abekawa and Gomi 2015). It has been shown that the MFR exhibits stronger responses when the limb is loaded (Saijo et al. 2005), similar to the gain scaling of stretch reflex responses. In particular they demonstrated significant correlations between the MFR and the background load and muscle activity for a variety of loading conditions. In contrast, our results showed no significant change in gain with respect to background load. Although we only examined this with eight subjects, similar numbers of subjects demonstrated highly significant slopes in all other experiments. This raises an intriguing question as to whether these two visuomotor feedback responses arise through distinct pathways which could explain these differences in the scaling of the response.

In this study we examined whether the sensorimotor control system is able to tune the rapid visuomotor feedback responses to environmental dynamics as part of the adaptation process. That is, to tune them to the environment in order to provide part of the adaptation to the dynamics. Several previous studies have shown evidence that feedback responses are modulated depending on the environment (Franklin et al. 2007, 2012; Wagner and Smith 2008; Kimura and Gomi 2009; Krutky et al. 2010; Ahmadi-Pajouh et al. 2012; Kobak and Mehring 2012; Yousif and Diedrichsen 2012; Cluff and Scott 2013; Diamond et al. 2015). Some of these studies have shown that feedback responses to physical perturbations after adaptation elicit responses that appear to be suitable for the change in environmental dynamics, but the measurements could not be separated from voluntary responses (Franklin et al. 2007; Wagner and Smith 2008) or limb admittance (Yousif and Diedrichsen 2012). Moreover, many of these studies involve changes in the background muscle activity which means that any change in feedback gain is difficult to dissociate from the effect produced by

gain scaling. In order to avoid these issues, a recent study measured the feedback responses by applying perturbations prior to the start of movement to examine the feedback component alone (Ahmadi-Pajouh et al. 2012) finding changes in the long latency feedback gain in the preparatory period prior to the movement, similar to the finding that gains are affected by the decision process (Selen et al. 2012). However, changes in the feedback responses during the postural phase prior to movement initiation does not indicate that the feedback gains are utilized as part of the adaptation to the dynamic environment. In order to address all of these issues, Cluff and Scott (2013) utilized a novel approach to the experimental design. They had subjects adapt to a force field in two directions such that no adaptation was necessary in a third movement located in the middle. Despite no changes in the background activity for movements in this middle movement direction, the long latency feedback gains were increased as subjects adapted to the force fields, with the feedback gain peaking at the end of the adaptation process. Another approach, which we use here, is to study rapid visuomotor feedback responses during adaptation (Franklin et al. 2012; Kobak and Mehring 2012), as these do not exhibit gain scaling.

These previous studies have shown that feedback gains are changed after force field adaptation or learning of novel dynamics. However, only a few of these studies have been able to clearly demonstrate that the change in the feedback responses are appropriate for the change in the environmental dynamics, with differential feedback gains for different environments. Cluff and Scott (2013) showed that the size of the stretch reflex was modified with the size of the viscous load learned in other parts of the workspace. Later, it was shown (Diamond et al. 2015) that subjects adjusted their grip force according to the learned dynamics of the environment when visuomotor perturbations of the hand location or target were imposed. Here we expand on these results by modifying the resistive force of the background force field. In Experiment 2, we introduced three levels of resistive viscosity which meant that lateral perturbations would require larger or smaller force responses in order to return the hand to the unperturbed trajectory. The feedback responses were

732 appropriately increased or decreased according to the dynamics suggesting that adaptation
733 also involved the tuning of the feedback gains to the dynamics. We recently showed that
734 rapid visuomotor feedback gains can be independently modulated to leftwards and
735 rightwards perturbations when different task-relevant or task-irrelevant sensory
736 discrepancies are applied to the left or right of the movement (Franklin et al. 2014). More
737 recently it has been shown that visuomotor reflexes elicited through target jumps are also
738 modulated by learning a distorted sensorimotor map imposed through visuomotor rotations
739 (Hayashi et al. 2016). We extended this work by demonstrating that feedback adaptation to
740 environmental dynamics also exhibited such independent modulation, where the feedback
741 responses were tuned differentially to rightwards and leftwards perturbations. Moreover, the
742 relative increase and decrease in feedback responses were appropriate for the changes in
743 the force field which only acted laterally to the direction of the movement. Therefore our work
744 extends previous results by clearly demonstrating that the visuomotor feedback responses
745 are tuned within the involuntary window to the dynamics of the environment. What is not yet
746 clear, however, is whether this adaptation of the feedback responses is part of the adapted
747 feedforward motor memory (Wagner and Smith 2008) or is an independent and dissociable
748 mechanism of adaptation (Yousif and Diedrichsen 2012).
749
750 We suggest that there are at least two computational components to the measured feedback
751 gains during adaptation to novel dynamics. Visuomotor feedback responses during
752 adaptation to a curl force field showed an initial rapid increase in feedback gains that was
753 gradually reduced to a lower plateau as the subjects adapted to the force field (Franklin et al.
754 2012). Thus after the initial increase, the feedback gains were reduced as the predictive
755 model was learned. However, in a later study it was shown that stretch reflexes are gradually
756 modified during learning, increasing in parallel to the predictive model (Cluff and Scott 2013).
757 While these two results may initially appear conflicting, we propose that they highlight two
758 computational components of feedback modulation: reactive control and predictive control.
759 Faced with uncertainty about the environment, the sensorimotor control system upregulates

a (likely default) pattern of feedback gains - what we term the reactive feedback system. This rise in feedback gains parallels the increase in co-contraction (Franklin et al. 2003, 2012). However, even in these first movements, the sensorimotor system is already learning the dynamics, gradually tuning the predictive controllers (Milner and Franklin 2005; Sing et al. 2009), including predictive feedback gains to the environment. Here we have shown further evidence that these predictive feedback gains can be tuned appropriately the dynamics, even differentially tuned on either side of the reaching movement.

Why might these initial, reactive, responses be decreased as learning proceeds? In the case of co-contraction, reduction likely occurs to decrease the metabolic cost of the movement (Huang et al. 2012; Huang and Ahmed 2014). However the metabolic cost of increased visuomotor feedback gains would be very small, not even requiring attentional demands for hand motion (Reichenbach et al. 2014). On the other hand, the visuomotor feedback systems can be affected by distractors: producing incorrect responses to visual movement of objects. Therefore, high feedback gains may be limited to avoid increased responses to distractors.

In the second experiment, the visuomotor feedback gains were significantly larger in the unstable environment compared to the stable condition. Such feedback gain increases for unstable dynamics have been shown previously for stretch reflex responses during reaching (Franklin et al. 2007) and isometric tasks (Krutky et al. 2010). In unstable environments, uncertainty in the internal model of the dynamics and increased unpredictability overall is likely maintained even after training. Therefore in these environments, one expects overall increased co-contraction and stiffness (Burdet et al. 2001; Franklin et al. 2003) along with these higher feedback gains. Such changes allow rapid responses to any unpredictable movements due to the instability. Here we show that we also find higher visuomotor feedback gains along with the previously shown stretch-dependent gains.

We examined the feedback gains over two intervals: the first corresponding to an rapid involuntary response (180–230 ms), and the second to a slower response (230-300 ms) which may either be involuntary or a mixture of involuntary and voluntary responses. The early interval was conservatively determined (Franklin and Wolpert 2008) using a voluntary reaction task (Day and Lyon 2000) to determine an interval which avoided any voluntary responses. There is some discussion (Franklin 2016) about whether these responses occur through a direct subcortical pathway through the superior colliculus (Reynolds and Day 2012) or a cortical pathway (such as through PMd). Different neural pathways likely produce responses at different delays relative to the initial perturbation and may also show different responses or controllability. We found that the visuomotor feedback gains were tuned appropriately to perturbations to either side of the reaching movement, but that this differentiation occurred later than the initial response. It might be that this more complex 'smart' feedback response indicates a more cortical pathway acting at a delay relative to the earliest response, while the initial response arises through a direct subcortical structure. However, any complex response depending on both internal models of the dynamics and body state might be expected to require intermediate neural layers and more synaptic connections increasing the response time. The separation of the analysis into two intervals does not suggest that each corresponds to a separate pathway involving different neural structures. It is simply performed in order to have one early interval in which we can avoid any voluntary response and a second interval in which we expect to see more gain modulation which might also have a voluntary component.

Modulation of the feedback responses according to the environmental dynamics is appropriate when we consider the optimal feedback control theory of motor control (Todorov and Jordan 2002; Scott 2004; Todorov 2004). According to this theory, movement arises through the appropriate selection of time varying feedback gains for each task that minimizes a mixed cost function of terms such as accuracy and energy. This theory therefore emphasizes the critical role that feedback responses have in generating

816 movement, and several studies have found evidence of such flexible, goal-directed feedback
817 responses (Liu and Todorov 2007; Dimitriou et al. 2013; Nashed et al. 2014). Together these
818 predict that the feedback responses should adapt as we learn new skills (Scott 2012). Here
819 we have provided further support that the feedback responses are tuned according to the
820 environment during adaptation. After adaptation to novel force fields, subjects normally only
821 compensate for around 80% of the environmental dynamics (Smith et al. 2006; Sing and
822 Smith 2010; Howard et al. 2012) such that the movement trajectories remain slightly curved.
823 This has been suggested to arise as these curved trajectories assist in reducing the
824 metabolic cost of the movements (Izawa et al. 2008), a consistent finding in the process of
825 adaptation (Huang et al. 2012; Huang and Ahmed 2014). That is, Izawa and colleagues
826 suggested that these S-shaped trajectories are the optimal solution to the force field,
827 producing initial overcompensation to the force field when the forces are low and allowing
828 the field to bring the hand back towards the target. In this optimal feedback control
829 framework, the feedback gains must then be tuned according to the dynamics in order to
830 produce the appropriate modifications in the trajectories. However, it has also been
831 suggested that this lack of complete compensation to the environmental dynamics may arise
832 due to the balance between the learning and forgetting rates of adaptation (Scheidt et al.
833 2000; Smith et al. 2006; Franklin et al. 2008), where this adaptation occurs through
834 feedforward pathways. In this case, when compensation to the environmental dynamics is
835 not complete, then the feedback responses may need to be adjusted in order to ensure that
836 the movement can still reach the goal or successfully complete the task. These feedback
837 gains therefore would be expected to be tuned to the dynamics, such that errors in the
838 movement can be corrected appropriately. As changes in the feedback gains should be less
839 costly metabolically compared to changes in muscle cocontraction, modulating the feedback
840 pathways will provide an efficient mechanism for the control and adaptation of movement.
841 Thus both interpretations for partial force field adaptation suggest a role for feedback gains
842 in adaptation to novel dynamics.
843

Our results reveal that feedback gain learning is indeed a critical part of dynamical adaptation, where feedback gains are tuned to the environmental dynamics. This opens up new questions in the mechanism of adaptation, specifically the mechanism by which the sensorimotor control system learns and tunes the feedback responses to the external environment.

851 **Figure Captions**

852

853 Fig 1. Experimental setup. *A:* The seated subject grasped the robotic manipulandum (vBOT)
854 while visual feedback was presented veridically using a top mounted monitor viewed through
855 a mirror. The subject's forearm was supported by an airsled. *B:* The visual perturbations
856 (probe trials) used to examine the magnitude of the rapid visuomotor feedback responses in
857 experiments 1 and 2. On randomly selected reaching trials, the hand was constrained
858 physically to a straight line to the target (mechanical channel) while the visual representation
859 of the hand (cursor) was jumped laterally away from the actual hand location for 250 ms
860 before being returned. *C:* The five force fields used in Experiment 2 shown as vector fields
861 as a function of hand velocity. The central column shows the three resistive force fields that
862 resist motion in any direction in proportion to velocity (top: low resistance; middle: medium
863 resistance; bottom: high resistance). The central row shows the three force fields with
864 identical resistance in the direction of movement, but which vary in the resistance in the
865 direction orthogonal to movement (left: mechanical channel; middle: medium resistance;
866 right: unstable assistance).

867

868

869 Fig 2. Experimental setup for experiment 3. *A:* The equal resistive force field is matched in
870 resistance (proportional to velocity) to motions to the right or left of the reaching movement
871 but does not resist motion in the direction of the movement. *B:* The leftwards resistive field
872 resists motion only in the leftwards direction proportional to the velocity. *C:* The rightwards
873 resistive field resists motion only in the rightwards direction. *D:* On normal reaching
874 movements in each of the three fields, the visual location of the hand was shifted to one of
875 seven locations between -6 and 6 cm at the halfway point of the movement. Subjects had to
876 correct for this shift and bring the cursor into the target by the end of the movement. *E:* The
877 visual perturbations (probe trials) used to examine the magnitude of the rapid visuomotor
878 feedback responses. On random reaching trials, the hand was constrained physically to

reach in a straight line towards the target (mechanical channel) while the visual representation of the hand (cursor) was jumped laterally away from the actual hand location for 250 ms before being returned. The onset of this perturbation was the halfway point of the movement.

Fig 3. Measures of adaptation to the six background loads (experiment 1). The background force was changed every 30 blocks (271 trials) and the order of the forces were randomized across subjects. The black lines indicate the mean measure, collapsed across different background loads to show learning within a background load block. *A:* The maximum perpendicular error of the hand (MPE) collapsed across the six background loads (mean ± SE across subjects) as a function of block number. The colored error bar plot shows the MPE (mean ± SE across subjects for last 25 blocks) for each background load separately. *B:* The success rate as a function of block number. *C:* The movement duration across blocks. The desired duration was 0.700 ± 0.075 s. *D:* The peak velocity.

Fig 4. Rapid visuomotor feedback responses during reaching with a constant background load (Experiment 1). *A:* In each condition, one of six different levels of resistive force was applied to the subjects' hand by the robotic system throughout the movement. *B:* The mean force responses to visual perturbations (difference in force produced on left and right perturbation on probe trials) for each of the six force levels (mean ± SE across subjects) are shown aligned to the onset of the perturbation. The color corresponds to the background load. The grey regions illustrate the time windows over which the force response was quantified. *C:* Mean ± SD force response over the early time window (180-230 ms) corresponding to an involuntary period. *D:* Mean ± SD force response over the late time window (230-300 ms). *E:* The mean force responses to visual perturbations (probe trials) for

left (positive going traces) and right (negative going traces) perturbation directions plotted separately. *F:* Mean ± SD force response over the early window by perturbation direction for left and right perturbations. *G:* Mean ± SD force response over the late window by perturbation direction.

Fig 5. Measures of adaptation to the five viscous force fields (experiment 2) - same format as Fig 3. The black lines indicate the mean measure, collapsed across different conditions, in order to show the change within the time of the experiment. Error Bars are mean ± SE across the last 25 blocks in each force field. *A:* The maximum perpendicular error (MPE) (mean ± SE) across the five fields. *B:* The success rate. *C:* The movement duration. *D:* The peak velocity.

Fig 6. Rapid visuomotor feedback responses during reaching in viscous force fields (Experiment 2). *A:* The mean force response (± SE) on probe trials for the three levels of resistive viscous force fields (-15: light blue; -30: blue; -45: dark blue). *B:* Mean ± SD force response over the early time window (180-230 ms) corresponding to an involuntary period for the fields in A. *C:* Mean ± SD force response over the late time window (230-300 ms). *D:* The force response on probe trials in the three force fields with different lateral stability conditions (mechanical channel: green; resistive viscous field -30 N/m/s: blue; assistive viscous field +10 N/m/s: purple). *E:* Mean ± SD force during the early time window. *F:* Mean ± SD force response during the late time window. Statistically significant differences between the conditions were tested with the Tukey-Kramer multiple comparisons test (* $p<0.05$; ** $p<0.01$).

Fig 7. Measures of adaptation to the equal, leftward resistive and rightwards resistive fields (experiment 3). The black lines indicate the mean measure, collapsed across different

conditions, in order to show the change within the time of the experiment. Error Bars are mean ± SE across the last 45 blocks in each force field. *A:* The maximum perpendicular error (MPE) (mean ± SE). *B:* The success rate. *C:* The movement duration. *D:* The peak velocity.

Fig 8. Corrective responses on the non-probe trial movements in the equal (left column), leftward resistive (middle column) and rightwards resistive (right column) fields (Experiment 3). *A:* The lateral (x-axis) cursor position as a function of the time from the visual shift that occurred at half of the movement distance. The mean (± SE) across subjects is shown for each of the seven visual shifts ranging from -6 cm (leftward shift: light green) to +6 cm (rightward shift: dark green). *B:* Lateral acceleration of the hand (mean ± SE) for each of the seven visual shifts as a function of time from shift onset. *C:* Mean ± SD of the lateral hand acceleration between 180-280 ms after the onset of the visual shift. *D:* Lateral force produced by the hand (mean ± SE) for the seven visual shifts. *E:* Mean ± SD of lateral hand force between 180-280 ms after visual shift onset. *F-J:* Same as A-E for the leftward resistive force field (rightward shifts: dark red; leftward shifts: light red). *K-O:* Same as A-E during the rightward resistive force field (rightward shifts: dark blue; leftward shifts: light blue).

Fig 9. Rapid visuomotor feedback responses during reaching in the equal, leftward resistive and rightwards resistive fields (experiment 3). *A:* The mean force response (± SE) on probe trials in the three force fields (equal: green; leftwards resistive: red; rightwards resistive: blue) for the rightward (dark colors) and leftward (light colors) visual perturbations. Responses have been subtracted from the zero perturbation condition in each force field. *B:* Mean ± SD of the force response over the early and late time windows. *C: top:* difference in

force responses to the leftward perturbations for the rightward (light blue) and leftward resistive force fields (orange) relative to the equal force field. The difference between these 2 measures was examined using ROC analysis to determine the time point at which the signals could be discriminated by an ideal observer. *bottom:* The vertical axis represents the probability that an ideal observer could discriminate between the responses in the two force fields. The green curve is the area under the ROC based on each subject's mean response. The solid blue line illustrates the dog leg fit which is used to determine the onset of the significant difference (large red circle). ROC analysis was also performed separately for each subject (small red circles). *D:* Differences in force responses for the rightward perturbations and the associated ROC analysis.

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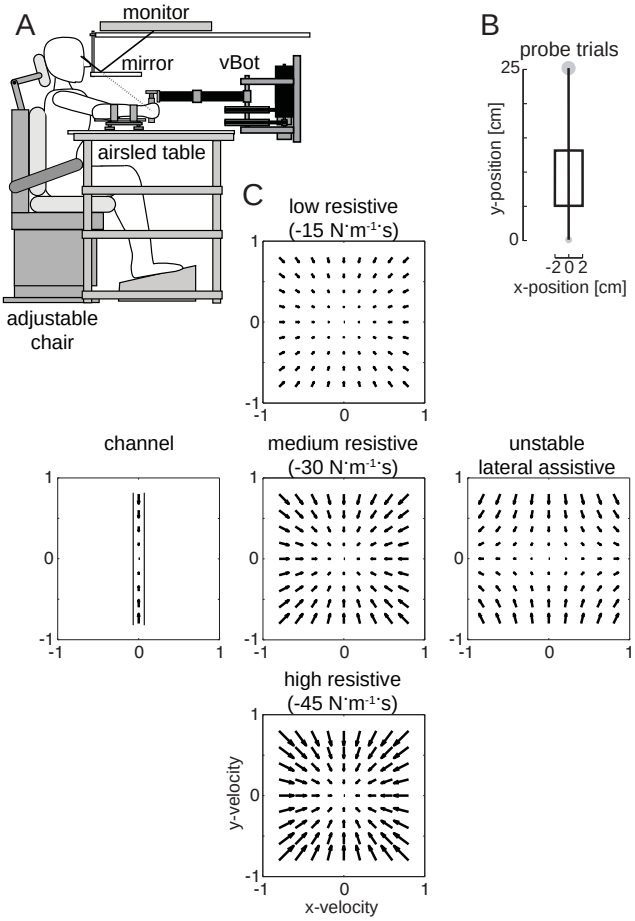
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vBot
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B
probe trials
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y-position [cm]
-2 0 2
x-position [cm]
C
low resistive
(-15 N·m-1·s)
channel
medium resistive
(-30 N·m-1·s)
unstable
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high resistive
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x-velocity
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0
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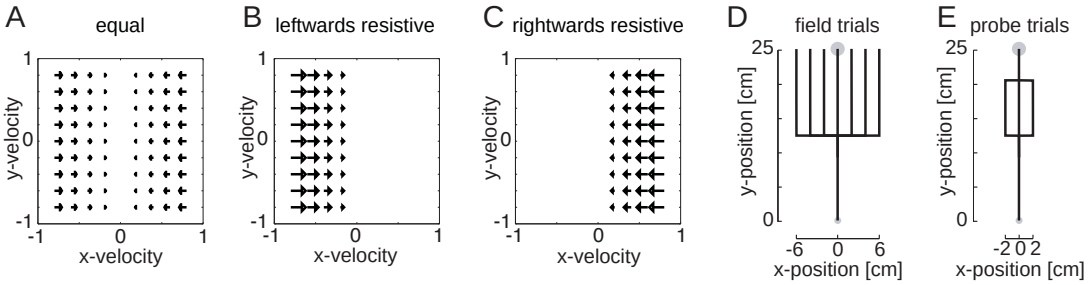
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equal
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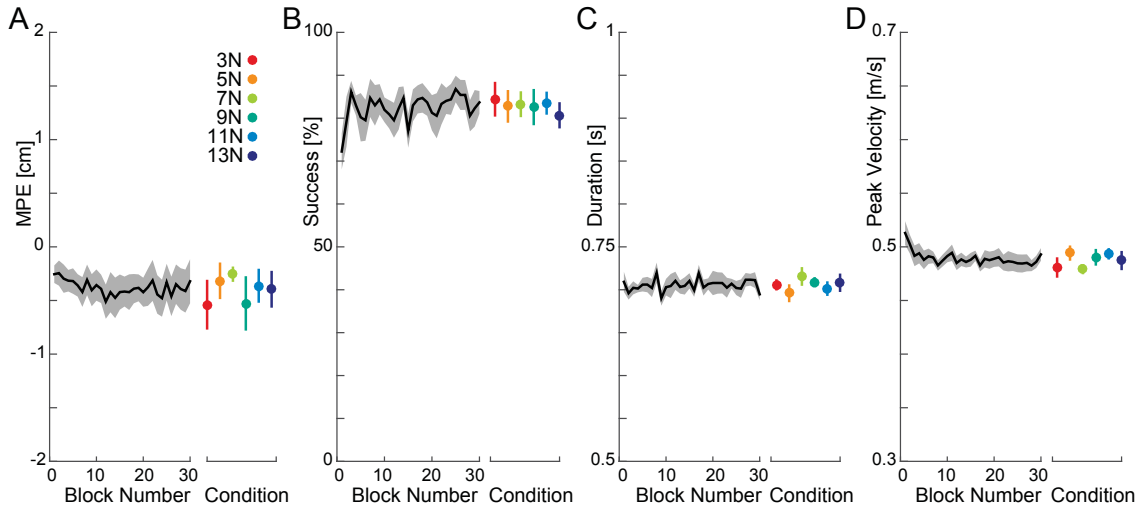
0
-1
25
6
2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B
C
D
MPE [cm]
Success [%]
Duration [s]
Peak Velocity [m/s]
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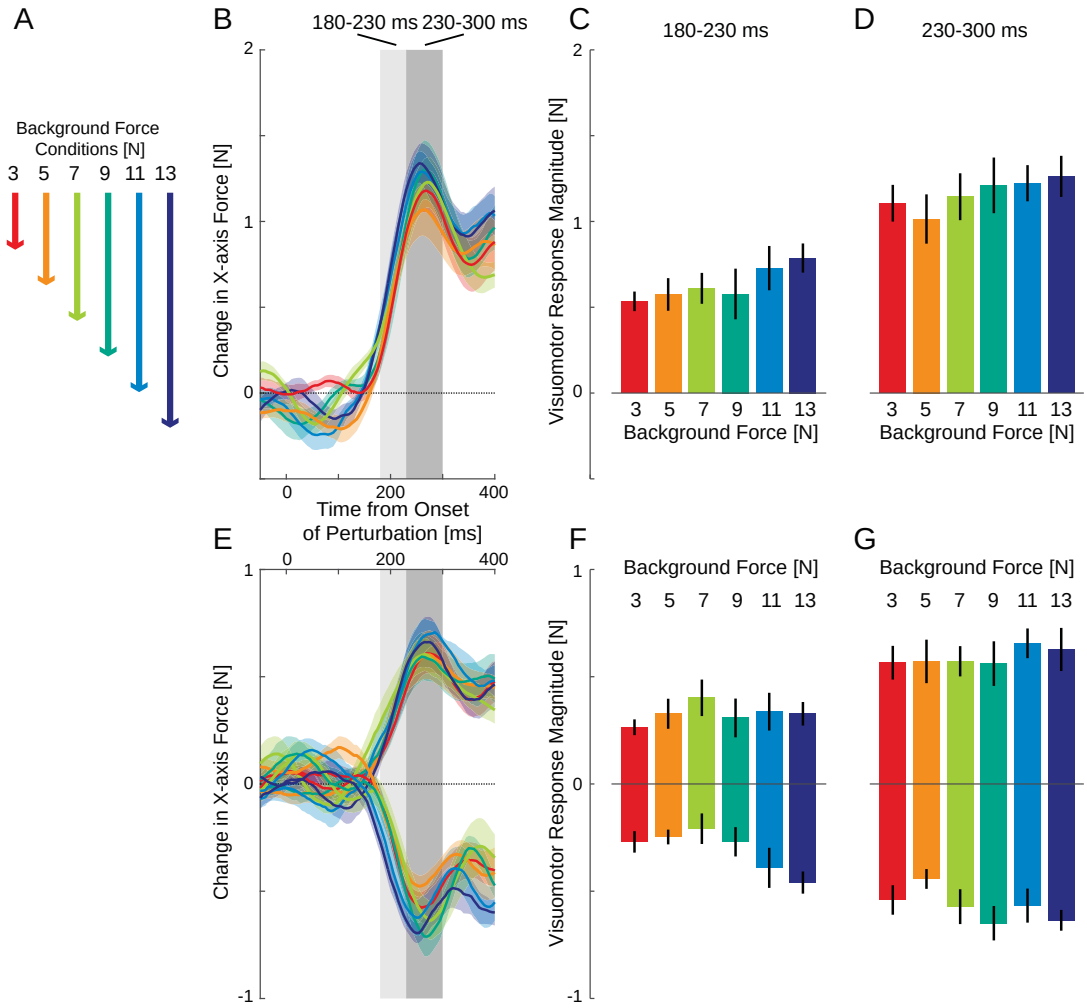
5N
7N
9N
11N
13N
Block Number
Condition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Background Force
Conditions [N]
3 5 7 9 11 13
B
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Change in X-axis Force [N]
2
1
0
0
200
400
Time from Onset
of Perturbation [ms]
C
180-230 ms
Visuomotor Response Magnitude [N]
2
1
0
3 5 7 9 11 13
Background Force [N]
D
230-300 ms
3 5 7 9 11 13
Background Force [N]
E
0
200
400
Change in X-axis Force [N]
1
0
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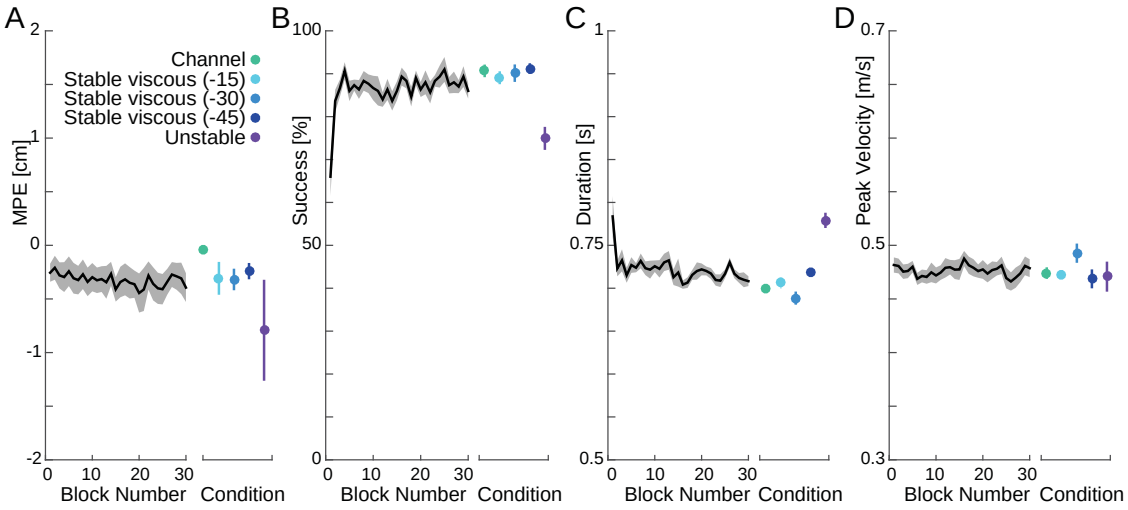
Background Force [N]
3 5 7 9 11 13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B
C
D
Channel
Stable viscous (-15)
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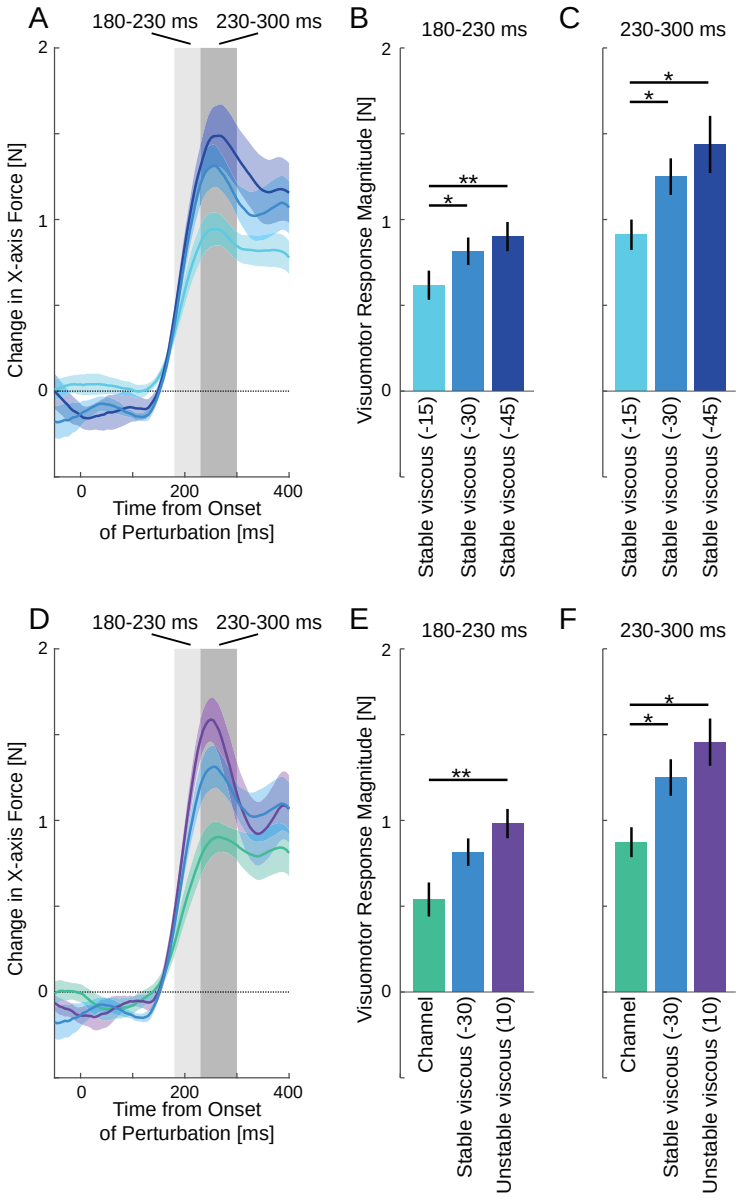
Unstable
MPE [cm]
Success [%]
Duration [s]
Peak Velocity [m/s]
Block Number
Condition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Time from Onset
of Perturbation [ms]
B
180-230 ms
Visuomotor Response Magnitude [N]
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C
230-300 ms
D
E
F
Channel
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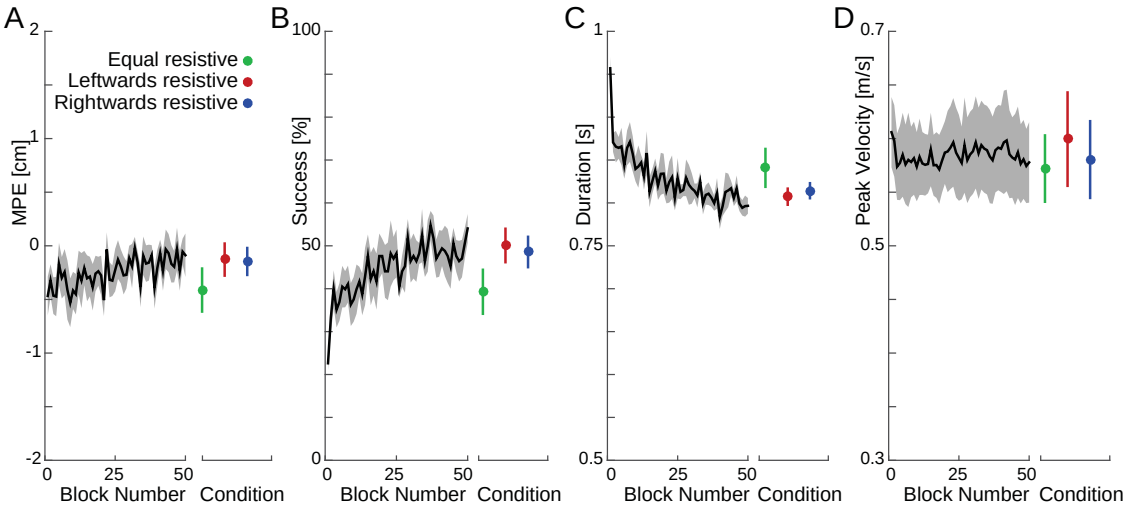
Unstable viscous (10)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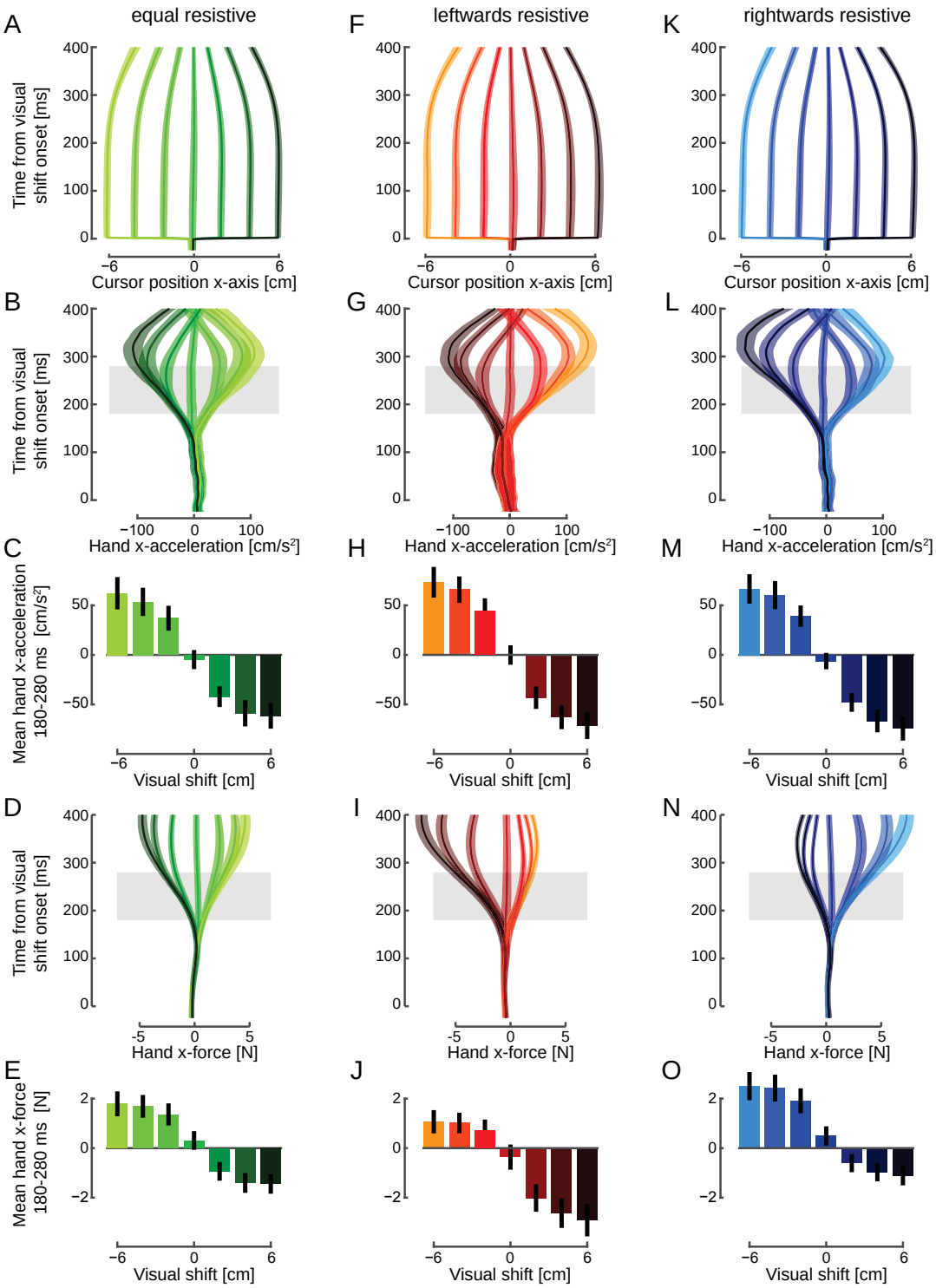
Duration [s]
Peak Velocity [m/s]
Block Number
Condition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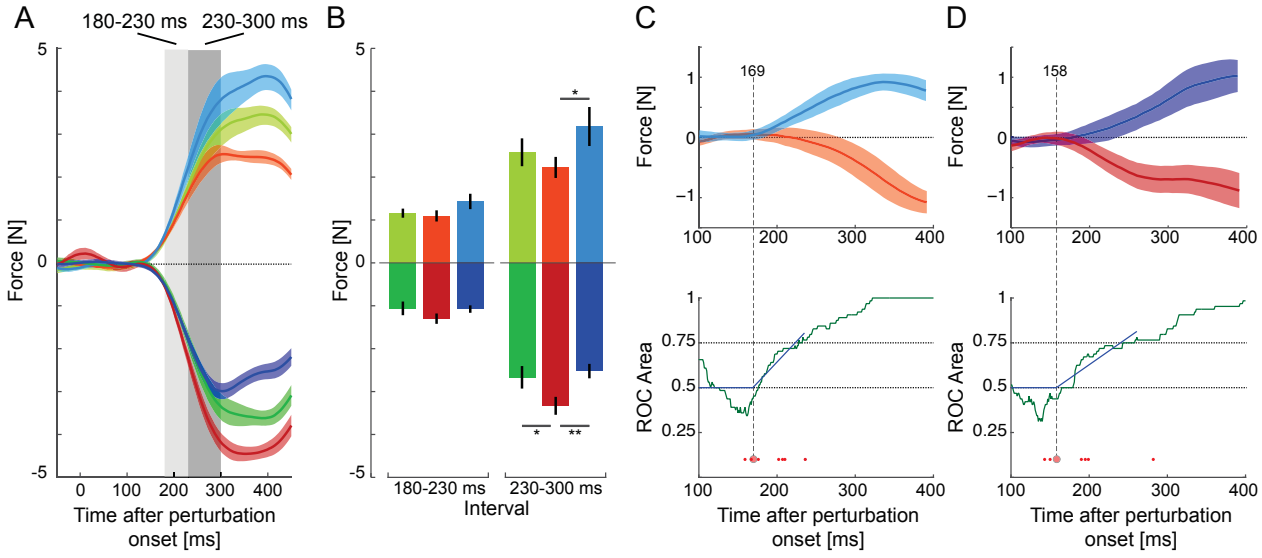
F
leftwards resistive
K
rightwards resistive
Time from visual shift onset [ms]
Cursor position x-axis [cm]
B
G
L
Hand x-acceleration [cm/s²]
C
H
M
Mean hand x-acceleration 180-280 ms [cm/s²]
Visual shift [cm]
D
I
N
Hand x-force [N]
E
J
O
Mean hand x-force 180-280 ms [N]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230-300 ms
Force [N]
Time after perturbation onset [ms]
B
Force [N]
180-230 ms
230-300 ms
Interval
C
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Force [N]
ROC Area
Time after perturbation onset [ms]
D
158
Force [N]
ROC Area
Time after perturbation onset [ms]